MATING BEHAVIOR AND SOCIAL STRUCTURE IN LOLIGO PEALII

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In the course of studies on embryological development of the squid, *Loligo pealii,* observations of the social behavior and mating reactions of this species were made. Observations made in the laboratory were confirmed by watching squid in their natural habitat. These studies have revealed a method for artificially stimulating mating and subsequent egg-laying. It is thus possible to have a reliable source of squid eggs, at convenient times, in the laboratory. Drew (1911) made extensive observations on copulation and egg-laying in *Loligo pealii* but, to the author's knowledge, nothing has been recorded on mate selection and social structure in this species.

Squid are particularly suitable for a study of social behavior for a number of reasons. They are pelagic and gregarious. Since there are no territorial separations, there is ample opportunity for a maximum of intraspecific interaction and, therefore, for the development of a social structure. They possess a moderate amount of intelligence which would enhance the establishment of social structure. Other than a few scattered observations on the Octopoda, very little has been published on the social behavior of the Cephalopoda. This paper is an attempt to show that *Loligo pealii* has a social structure concerned with its mating behavior.

Materials and Methods

The animals used in this study were captured in fish traps in the vicinity of Woods Hole or Barnstable, Massachusetts, in the summers of 1960 and 1961. Late in the summer of 1961 some animals were used that had been captured in fish traps off the coast of Rhode Island. There seemed to be some minor differences in these two populations, indicated by their interaction, but their intra-population interaction was the same. The animals were all sexually mature but varied in mantle length from about six to ten inches. The males appeared to be slightly larger than the females. The animals were obtained from the Supply Department of the Marine Biological Laboratory, usually shortly after their capture and at most one day thereafter. They were kept in a 2½ by 6 foot fiberglass tank filled to a depth of 12 inches with rapidly running sea water. Usually from four to ten animals were kept in such a tank at one time without apparent overcrowding. Usually more males were present than females, although in some cases the situation was reversed. The animals were fed about two *Fundulus heteroclitus* per squid, usually daily. Under these conditions the squid survived about five days. In one case a male survived for seventeen days in a tank that was undisturbed except for periodic feeding.

Males and females are easily distinguished by the presence of the white testis in

the male, the slimmer outline of the males, and the presence of the bright orange accessory nidamental gland visible through the mantle of the female. Individuals of either sex could be distinguished by their size or by characteristic wounds and scars on their mantles.

The animals were stimulated with a naturally laid egg mass tied to a cotton cord and lowered into one corner of the tank. An artificial egg mass was constructed of water-filled tubing made of polyethylene sheet fused together at the edges. A small amount of phenol red was added to the water used in the tubing to give it an orange color like that of the egg mass. Other animals were introduced to an existing group by slowly submerging a bucket containing the new animals into the tank and allowing them to swim out. The observations of squid in nature were made from a fixed wharf or an anchored boat in shallow water after dark. These observations were made with the assistance of a fixed incandescent lamp.

Observations

Initiation of sexual behavior

Normally, the captive squid swim parallel to each other in a small school moving back and forth in synchrony. There is no apparent social order to their position in these small schools. The males and females move about in the tanks paying no apparent attention to each other. Since these animals were chosen randomly from a much larger group (about 30–50), any prior social pattern is assumed to have been broken. There seems to be no particular dominance in feeding behavior since any *Fundulus* offered is taken by the nearest squid. No other evidence of any social pattern has been observed and if any such structure existed at this time it was latent. Therefore, it is assumed that mate selection had not taken place in this condition. In these circumstances a stimulus could be presented and characteristic responses observed.

If a naturally laid egg mass was tied to a string and placed in one corner of the tank, the squid almost immediately "broke formation" and investigated the egg mass. This response began when the animals swam rapidly toward the egg mass, formed their arms into a cone, and pointed at the egg mass. Occasionally the egg mass would be flushed with spurts of water from the funnel of an approaching squid. One animal after another would dart up to the egg mass and "feel" it with its arms. Then each would rapidly dart away and rejoin the group. Two individuals would occasionally approach the egg mass at the same time. Both males and females would show this response which would occur within about twenty seconds after the introduction of the egg mass.

This stimulus seemed to be completely visual because of the speed with which the squid responded. This hypothesis was checked by using an artificial egg mass of polyethylene tubing. This artificial egg mass elicited the same response as a real egg mass. The animals investigated and felt it but responded abnormally by flushing it repeatedly with spurts of water from their funnels and by swimming excitedly to and fro. However, this was still followed by normal mate selection and the establishment of a hierarchy. Usually the egg string would be held in the arms for several minutes and then dropped on the bottom of the tank. In two cases egg capsules were actually laid on the artificial egg mass although the female made

several approaches before finally attaching the egg string. Further evidence of the visual nature of this stimulus can be drawn from the fact that in the absence of an egg mass, egg strings would be attached to anything that resembled an egg mass. Several times egg strings have been deposited on the arms of a dead squid left in the tank. In cases of deprivation of stimulus the squid will even investigate the extended fingers of a human hand placed in the tank (not recommended).

The stimulus worked best on squid that had not been known to have bred recently, hence the necessity of getting the animals as soon as possible after their capture. If deprived of stimulus for a long period of time, females would eventually drop egg strings but made no apparent attempt to form an egg mass unless a nucleus of egg strings accumulated by chance at the tank drain.

This response to an egg mass has been observed in nature by dangling an egg mass on a string in front of a school of squid. Egg-laying has occurred in these egg masses.

Establishment of a hierarchy

The investigative behavior was followed by dominance determination behavior. This began by the males raising one median arm a few centimeters above the rest of the arms and waving it. Sham battles usually followed in which the males rushed at each other but did not actually touch each other. At the same time they developed dark brown lateral areas at the base of the arms. This color pattern seemed to be characteristic of sexually aroused male squid. During this time a given male would place himself between the rest of the group and a female of his choice. Any approaching male would be threatened by a waving of the median arm. If the approaching male was persistent, he would be driven off by rushes from the selecting male. In cases where the intruder was extremely insistent, the two males would sometimes bump tails and display characteristic dark colored spots along the lateral margins of the fins. These spots were not observed at any other time on any male. This has been interpreted as a further warning sign. In a relatively few cases there was actual contact between two males. In these cases the males rushed at each other and one grasped the other around the mantle. In three observed cases the arms interlocked and in one case the tip of an arm was bitten off. This behavior continued between all the males in the tank until one male was established as the dominant male. Other males appeared subordinate to this male. The subordinate males each selected a female and would undergo similar combat among themselves. An individual's position in the social structure seemed roughly correlated with its size. Since there were fewer females than males in the tank, a few males did not have mates. Only rarely did one of the mateless males succeed in displacing a mated male. The squid taken from the traps at Rhode Island seemed to be more aggressive and would challenge and displace larger squid taken from the Cape Cod population. As the physical conditions of a male deteriorated the same social structure remained until he reached a completely defenseless state and another male could take over his female. If a new male was introduced to a group that had established a social structure he would be immediately challenged by the other males until he was integrated into the social structure. This would often result in a displacement of an established male and the displaced male would then displace his subordinate or, if in poor physical condition, be relegated to the

mateless group. Only rarely did any male attempt to change its mate spontaneously.

The behavior of the females was less active. Normally a female would show slight avoidance of a male but seemed to have no mate preference. While mate selection and challenging went on between males, females paid no apparent attention to the males. Once the social structure among males had been established the males attempted copulation with the females. Normally a female would resist by darting away quickly when the male attempted copulation. After a short interval the female usually accepted the male's advances and copulation followed.

Copulation and egg-laying

The behavior and events during copulation have been well described by Drew (1911) and only details not recorded there will be mentioned here. The male swam parallel to the female and moved back and forth exactly at the same time (assuming no other male intruded). The spots at the base of the arms of the male became intense. Occasionally copulation was preceded by the male reaching out with one arm and lightly touching the female on the mantle behind the head. There were two methods of copulation observed. Most common was the lateral method in which the male paralleled the female and grasped her around the mantle behind the head, the hectocotylized arm was placed into his own mantle, spermatophores picked up, and then transferred to the female by way of her funnel. This took about ten seconds. The second method of copulation involved a meeting of the male and female head to head and probably resulted in a transfer of the spermatophores to the buccal pouch. This method was infrequently observed.

Occasionally a female would strongly resist a male and would not permit copulation at all. This was usually done by swimming rapidly away or by struggling when the male grasped her. Rarely, if a male was very aggressive, the female would actively resist by grasping the male with her arms. On three occasions females have propelled themselves out of the tank in an attempt to escape an aggressive male. In cases where the females outnumbered the males a polygamous relationship would develop. In two cases, when males were in reduced physical condition, the females took the aggressive role and attempted to force copulation by grasping the male about the mantle. In one case an aggressive female could get no response and finally ate part of the male. Several times males displayed necrophilia (Daveian behavior) when no living females were available to them.

Copulation was usually followed by egg-laying. Drew (1911) has given an elaborate account of egg-laying and all that will be mentioned here is a brief account for the sake of completeness. After copulation the female approached the egg mass and again investigated it. An egg string was then passed from the funnel to the arms which encircled it. The female approached the egg mass and reached into the center and manipulated the egg string into place. One end of the egg string is free of eggs, narrower, and denser in composition. This end was intertwined in the egg mass with the tips of the arms so that the string was firmly enmeshed. If during this time the string was dropped the complete operation was continued as if nothing abnormal had happened. The female quickly retreated from the egg mass following the attachment of the egg string. A new egg string was then passed up

to the arms and the process repeated. In one case, seven females added 26 egg strings to one small egg mass of twenty strings in thirteen minutes.

Discussion

The major points of this paper are the nature of the stimulus of reproductive behavior and the resultant social structure. The stimulus was no doubt visual because of the speed at which the response occurred and the fact that objects having a resemblance to egg masses would cause such a response. It is the author's opinion that this stimulus elicits sexual behavior. This would explain the fact that egg masses are often found attached to *Fucus* or similar sea weeds. Several females deposit their egg strings on a common egg mass which agrees with this hypothesis. The report of vast beds of squid eggs off the California coast could also be explained by such a hypothesis (McGowan, 1954). Undoubtedly, there must be another stimulus that elicits the original mating that results in the formation of the original egg mass. This egg mass then elicits mating behavior in other squid. The nature of the original stimulus remains unknown and it is possible that this original mating occurs spontaneously.

The social structure in the males appears to be a classical peck order with an establishment of a dominant male able to resist all other males, and of a series of subordinate males. These subordinate males are able to resist males of a lower position but may be displaced by a male of higher position.

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Summary

1. Observations of *Loligo pealii* have shown the egg mass can stimulate sexual behavior. This stimulus apparently has a visual basis.

2. This stimulus is followed by establishment of a social hierarchy and by mate selection by the males. The males exhibit warning displays, sham battles, and mate protection during this time.

3. Normally the females respond passively but occasionally they will take an aggressive role.

4. This mating behavior results in copulation and egg-laying; thus a method for obtaining naturally laid eggs has been revealed.

LITERATURE CITED

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